RESISTANCE TO CHANGE AS A FUNCTION OF STIMULUS–REINFORCER AND LOCATION–REINFORCER CONTINGENCIES

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Pigeons responded on two keys in each component of a multiple concurrent schedule. In one series of conditions the distribution of reinforcers between keys within one component was varied so as to produce changes in ratios of reinforcer totals for key locations when summed across components. In a second series, reinforcer allocation between components was varied so as to produce changes in ratios of reinforcer totals for components, summed across key locations. In each condition, resistance to change was assessed by presenting response-independent reinforcers during intercomponent blackouts and (for the first series) by extinction of responding on both keys in both components. Resistance to change for response totals within a component was always greater for the component with the larger total reinforcer rate. However, resistance to change for response totals at a key location was not a positive function of total reinforcement for pecking that key; indeed, relative resistance to extinction for the two locations showed a weak negative relation to ratios of reinforcer totals for key location. These results confirm the determination of resistance to change by stimulus–reinforcer contingencies.
Key words: multiple schedules, concurrent schedules, stimulus–reinforcer contingencies, location–reinforcer contingencies, serial compound stimuli, resistance to change, pigeons

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If two discriminated operants are disrupted by prefeeding, by arranging alternative reinforcement either concurrently or successively, or by extinction, their resistance to disruption depends on baseline reinforcement parameters. Specifically, operants that are maintained by larger, more frequent, or more immediate reinforcers show greater resistance than their counterparts that are maintained by reinforcement of lower value (Harper & McLean, 1992; Nevin, 1974; Nevin, Mandell, & Atak, 1983).

Resistance to change has been shown to depend on Pavlovian stimulus–reinforcer contingencies rather than on operant response–reinforcer contingencies. For example, Nevin, Tota, Torquato, and Shull (1990) studied resistance to prefeeding, satiation, or extinction in components of multiple schedules. They found that the baseline rate of a target response was lowered by additional reinforcement. However, resistance to change of the same response was greater in components for which additional reinforcers were arranged noncontingently (Experiment 1) or contingent on responses on a second key that was lit with the same discriminative stimulus (Experiment 2). If response–reinforcer relations determined resistance to change for the target response, the additional reinforcers obtained from alternative sources would have no effect (or would weaken resistance). Instead, the results indicated that resistance to change was determined by the relations between discriminative stimuli that signaled components and the *total* reinforcement, summed over various sources. That is, additional reinforcers from alternative sources enhance the resistance of a target response. Similar results have been reported by Mace et al. (1990) and Cohen (1994) for human subjects, by McLean and Blampied (1995) for pigeons, and by Mauro and Mace (1996) for rats.

The conclusion that stimulus–reinforcer rather than response–reinforcer contingencies determine resistance to change is also supported by evidence from other paradigms (Nevin, 1984, 1992a; Nevin, Smith, & Roberts, 1987). However, one aspect of the Nevin et al. (1990) data did not conform to this conclusion. Specifically, their Experiment 2 found that for 2 of 3 subjects, responding was more resistant to disruption on the key cor-

related with relatively infrequent reinforcement in a concurrent-schedule component of a multiple schedule. The problem was that responding and reinforcement on both concurrent alternatives occurred in the presence of a single distinctive stimulus situation; thus, resistance to change should have been the same for both alternatives if it was determined solely by stimulus–reinforcer relations. Nevin (1992b) suggested that this discrepancy could be explained by the fact that the key on which greater resistance to change was exhibited was also the key on which reinforcers were obtained in other schedule components. He therefore argued that resistance to change depended on the correlation of reinforcement rate with both the component stimuli and with response location. On that basis, he was able to integrate the findings of research on resistance to change in a number of different paradigms.

As Nevin (1992b) stated, Experiment 2 of Nevin et al. (1990) was not designed to examine possible effects of location–reinforcer relations on resistance to change, and replication and extension are required. The present study was designed to compare resistance to change for responding on two keys that are available during each component of a multiple schedule. Over conditions in one series, the reinforcer totals for each key, summed over components, were varied systematically. In addition, a second series of conditions was arranged in which reinforcer totals for components, summed over the two response locations, were varied systematically. In both series, responding on both keys was disrupted by noncontingent reinforcement presented during intercomponent blackouts and, in Series 1, by extinction. Thus, the design permits separate quantification of the effects of component stimulus–reinforcer and location–reinforcer relations on resistance to change.

METHOD

Subjects

Four homing pigeons, with prior experience in multiple schedules in which two responses were available in each component, were maintained at 80% to 85% of their free-feeding weights. Water and grit were continuously available in home cages, where supple-

mentary feed of mixed grain was given when needed to maintain prescribed weights. Supplementary feed was given roughly 3 hr after experimental sessions.

Apparatus

Four similar experimental chambers (34 cm by 34 cm by 32 cm) each contained an interface panel with three response keys, one mounted centrally and the others 9 cm to either side of it, all 21 cm above the grid floor. The center key and houselight were not used. Pecks on either side key that exceeded approximately 0.15 N produced a relay click and extinguished for 50 ms the red or green lights illuminating the key from behind. A hopper containing wheat was mounted in the center of the interface panel 6 cm above the floor and was operated and lit with white light for 3 s during reinforcement. Scheduling and recording of all experimental events were accomplished using an IBM®-AT compatible computer running MED-PC® software and using MED Associates® interfacing.

Procedure

Subjects were trained in 45-min sessions, usually 7 days per week, in the chambers assigned to them for an earlier experiment. During the two multiple-schedule components, the two response keys were either both illuminated red or both illuminated green, except during reinforcement when both were darkened. Components remained in effect for 60 s (excluding time occupied by reinforcement) and were always preceded by 30 s of blackout, during which the chamber was darkened and response keys were inoperative. Variable-interval schedules used to maintain responding on each of the two keys comprised 12 intervals from the Fleshler and Hoffman (1962) progression, and were sampled at random without replacement. A response to either key that directly followed a response on the alternative key constituted a changeover and was never reinforced. In addition, changeovers started a changeover delay that prevented reinforcement of further responses for 3 s and that was restarted if another changeover occurred.

Resistance to change was tested several times in each of five conditions, summarized in Table 1. Before any resistance tests were conducted in a condition, responding was

Table 1

Variable-interval schedules in seconds, with associated reinforcer rates per hour in parentheses, for each key in each component for the five conditions in the experiment. Arranged log ratios of reinforcers summed across components for left and right keys (L/R) and across keys for Components 1 and 2 (C1/C2) are also given. Disruptors were either random-time food schedules operating during intercomponent blackouts or extinction of responding on both keys in both components, and they were in effect for various numbers of sessions, as shown. Note that Birds A5 and A6 ceased responding on the right key in Component 1 during Condition 3, and were tested in Condition 3a instead. During Condition 5, equipment failure necessitated restarting training for Bird A6.

| Condition | Component 1 | | Component 2 | | Arranged log reinforcer ratios | | Schedule in blackout | Sessions |
	Left	Right	Left	Right	L/R	C1/C2		
1	VI 40 (90/hr)	VI 120 (30/hr)	VI 120 (30/hr)	VI 40 (90/hr)	0	0	Extinction	40
	VI 40	VI 120	VI 120	VI 40	0	0	RT 25 (144/hr)	11
	VI 40	VI 120	VI 120	VI 40	0	0	Extinction	34
	VI 40	VI 120	VI 120	VI 40	0	0	RT 6.25 (576/hr)	2
	VI 40	VI 120	VI 120	VI 40	0	0	Extinction	16
	VI 40	VI 120	VI 120	VI 40	0	0	RT 6.25 (576/hr)	2
	VI 40	VI 120	VI 120	VI 40	0	0	Extinction	15
	VI 40	VI 120	VI 120	VI 40	0	0	RT 12.5 (288/hr)	11
	VI 40	VI 120	VI 120	VI 40	0	0	Extinction	15
	Extinction	Extinction	Extinction	Extinction			Extinction	7–8
2	VI 40 (90/hr)	VI 120 (30/hr)	Extinction	VI 30 (120/hr)	−0.22	0	Extinction	30
	VI 40	VI 120	Extinction	VI 30	−0.22	0	RT 25 (144/hr)	11
	VI 40	VI 120	Extinction	VI 30	−0.22	0	Extinction	34
	VI 40	VI 120	Extinction	VI 30	−0.22	0	RT 6.25 (576/hr)	2
	VI 40	VI 120	Extinction	VI 30	−0.22	0	Extinction	16
	VI 40	VI 120	Extinction	VI 30	−0.22	0	RT 6.25 (576/hr)	2
	VI 40	VI 120	Extinction	VI 30	−0.22	0	Extinction	15
	VI 40	VI 120	Extinction	VI 30	−0.22	0	RT 12.5 (288/hr)	11
	VI 40	VI 120	Extinction	VI 30	−0.22	0	Extinction	15
	Extinction	Extinction	Extinction	Extinction			Extinction	7–8
3a (Birds A5 and A6)	VI 40 (90/hr)	VI 120 (30/hr)	VI 40 (90/hr)	VI 120 (30 hr)	0.48	0	Extinction	30
	VI 40	VI 120	VI 40	VI 120	0.48	0	RT 6.25 (576/hr)	3
	VI 40	VI 120	VI 40	VI 120	0.48	0	Extinction	22
	VI 40	VI 120	VI 40	VI 120	0.48	0	RT 25 (144/hr)	11
	VI 40	VI 120	VI 40	VI 120	0.48	0	Extinction	17
	VI 40	VI 120	VI 40	VI 120	0.48	0	RT 12.5 (288/hr)	10
	VI 40	VI 120	VI 40	VI 120	0.48	0	Extinction	20
	Extinction	Extinction	Extinction	Extinction			Extinction	6
3 (Birds A7 and A8)	VI 40 (90/hr)	VI 120 (30/hr)	VI 30 (120/hr)	Extinction	0.85	0	Extinction	40
	VI 40	VI 120	VI 30	Extinction	0.85	0	RT 25 (144/hr)	11
	VI 40	VI 120	VI 30	Extinction	0.85	0	Extinction	34
	VI 40	VI 120	VI 30	Extinction	0.85	0	RT 6.25 (576/hr)	2
	VI 40	VI 120	VI 30	Extinction	0.85	0	Extinction	16
	VI 40	VI 120	VI 30	Extinction	0.85	0	RT 6.25 (576/hr)	2
	VI 40	VI 120	VI 30	Extinction	0.85	0	Extinction	15
	VI 40	VI 120	VI 30	Extinction	0.85	0	RT 12.5 (288/hr)	11
	VI 40	VI 120	VI 30	Extinction	0.85	0	Extinction	15
	Extinction	Extinction	Extinction	Extinction			Extinction	7–8
4	Extinction	VI 120 (30/hr)	VI 30 (120/hr)	Extinction	0.6	−0.6	Extinction	35
	Extinction	VI 120	VI 30	Extinction	0.6	−0.6	RT 12.5 (288/hr)	10
	Extinction	VI 120	VI 30	Extinction	0.6	−0.6	Extinction	20
	Extinction	VI 120	VI 30	Extinction	0.6	−0.6	RT 6.25 (576/hr)	7

Table 1

(*Continued*)

Condition	Component 1		Component 2		Arranged log reinforcer ratios		Schedule in blackout	Ses-sions
	Left	Right	Left	Right	L/R	C1/C2		
5	VI 40	VI 80	Extinction	VI 80	0	0.48	Extinction	25
(Birds A5,	(90/hr)	(45/hr)	Extinction	(45/hr)				
A7, and	VI 40	VI 80		VI 80	0	0.48	RT 12.5 (288/hr)	5
A8	VI 40	VI 80	Extinction	VI 80	0	0.48	Extinction	20
	VI 40	VI 80	Extinction	VI 80	0	0.48	RT 6.25 (576/hr)	7
(Bird A6)	VI 40	VI 80	Extinction	VI 80	0	0.48	Extinction	21
	(90/hr)	(45/hr)		(45/hr)				
	VI 40	VI 80	Extinction	VI 80	0	0.48	RT 12.5 (288/hr)	5
	VI 40	VI 80	Extinction	VI 80	0	0.48	Extinction	20
	VI 40	VI 80	Extinction	VI 80	0	0.48	RT 6.25 (576/hr)	5

maintained in baseline for 21 to 40 sessions. This was relaxed once subjects had extensive exposure to a condition, so that a minimum of 15 baseline sessions was conducted between tests. Baseline performances were assessed using data from the last 10 sessions before a disruptor was introduced. No formal stability criterion was used, but stability of performance in baselines was assessed by calculating standard deviations of response rates over the last 10 sessions. Resistance to change was assessed using two types of disruptors. First, response-independent reinforcers were sometimes delivered during intercomponent blackouts according to random-time (RT) schedules arranged by interrogating a probability gate every 0.5 s. These disruptor conditions were usually in effect for at least 10 sessions, except that only one to five sessions of disruption were conducted when a very high rate of response-independent reinforcement (576 per hour) was used. Second, in some conditions there were between six and 10 sessions in which reinforcers were withheld for both keys in both components (extinction).

The five conditions formed two series (refer to Table 1). In Series 1 (Conditions 1 through 3), the total of reinforcement for each key, summed over the two components, was varied over three conditions. The totals for the two components remained constant and equal to one another. In each condition, responding was disrupted by response-independent food arranged during blackout periods at rates of 144 per hour (RT 25 s), 288 per hour (RT 12.5 s), or 576 per hour (RT

6.25 s). At the end of each condition, responding was disrupted by six to 10 sessions of extinction, during which no responses were reinforced. In Series 2 (Conditions 3 through 5), the total of reinforcement summed over keys within each component was varied over three conditions. In each condition, responding was disrupted by response-independent food given at 288 per hour (RT 12.5 s) or 576 per hour (RT 6.25 s). The reinforcement schedules, disruptors, and the number of training sessions given in each condition are listed in Table 1 in the order of exposure.

RESULTS

Response and reinforcer rates were calculated, taking account of time occupied by reinforcement, for each of the last 10 sessions in predisruptor baselines. These rates were then averaged to give estimates of baseline performance. Rates were also calculated for each session conducted with disruptors present and were averaged for each disruptor condition to summarize performance. These mean rates in baseline and in disruption conditions are given in the Appendix (with their standard deviations) and confirm strong control by component stimuli over response rates on the two keys. Standard deviations for response rates over the last 10 sessions in baseline conditions were small, confirming satisfactory stability of performance before resistance tests were conducted. The results from the two series of conditions are described separately below.

Series 1: Effects of the Location–Reinforcer Contingency

Over conditions, the rates of reinforcement in Component 1 and the distribution of reinforcers between keys were both constant. In Component 2, the total rate of reinforcement was the same as that in Component 1, but the distribution of reinforcers between keys was varied across conditions. Birds A5 and A6 ceased responding on the right key in Component 1 during Condition 3, and the contingencies in Component 2 were modified before resistance tests were performed (see Table 1). Arranged log ratios of reinforcer totals varied over a range of 0.7 for Birds A5 and A6 and over a range of more than 1.0 for Birds A7 and A8.

Figure 1 shows the resistance functions for response rates in the constant component (Component 1). Three separate functions are shown, one for each of Conditions 1 through 3. If the number of reinforcers on a key in Component 2 affected resistance to change on the same key in Component 1, the slopes of these functions would differ. Specifically, functions in the first column would be steepest for open circles (Condition 2, low left total reinforcement), intermediate for squares (Condition 1, equal left and right total reinforcement), and shallowest for filled circles (Condition 3, high left total reinforcement). For the right key (third column), the order would be reversed. No such ordering of resistance to change was apparent in either the first or third columns. For the left key, slopes were rather similar for the three conditions, and the differences that did occur were not systematic over conditions. The rate of right-key responding was rather low overall, and proportions varied unsystematically with response-independent food both in terms of direction of change and in terms of ordinal relations among conditions. Thus, location–reinforcement relations had no effect on resistance to change of responding on either key in Component 1. Response rates in successive sessions of extinction (second and fourth columns of Figure 1) generally underwent orderly reductions, especially for the left key. Again, similar slopes occurred in each condition, and no systematic ordering of slopes across conditions was apparent.

The analysis given in Figure 1 compared resistance for each key across conditions that differed in terms of the distribution of reinforcers between keys when summed over components. Within-condition comparisons of resistance to change would be stronger than between-condition comparisons, but are difficult to make because both types of disruptor produced unsystematic changes in responding on the lean-reinforcement key. Accordingly, we summed response rates on each key across components in Conditions 1, 2, and 3 prior to calculating proportions. Figure 2 gives performance over sessions in the presence of each disruptor for Condition 1, expressed as a proportion of the summed rate in the 10 immediately preceding baseline sessions. In Condition 1, the total reinforcement for the left key (summed across components) was equal to that for the right key. Therefore, neither key was associated with greater reinforcement than the other, and no differential resistance to change should be apparent. Bird A5 showed greater resistance to RT food on the left key, and Bird A6 showed greater resistance on the right key. The remaining 2 subjects showed no consistent differences in resistance between the two keys. When extinction was used as the disruptor, Birds A5 and A8 showed opposite differences in resistance, and A6 and A7 showed no differences. Overall, the data from Condition 1 revealed no consistent differences between keys in terms of resistance to change.

Figure 3 gives the same analysis for Conditions 2 and 3, over which the relative reinforcer total for the left key versus the right key was varied. In Condition 2, the overall rate of reinforcement for the left key was lower than that for the right by a factor of almost two. No subject showed consistently greater reduction of responding on the left key during response-independent food disruption or during extinction. The right panels of Figure 3 present data from Condition 3, in which total reinforcement was greater for the left key by a factor of at least three. The results are consistent with those for Condition 2, although the data were more variable, especially for the right key, on which responding often increased when response-independent food was scheduled. Although resistance to change appeared to be greater for the right key in two tests using moderately low rates of RT food in blackout, this was not borne out
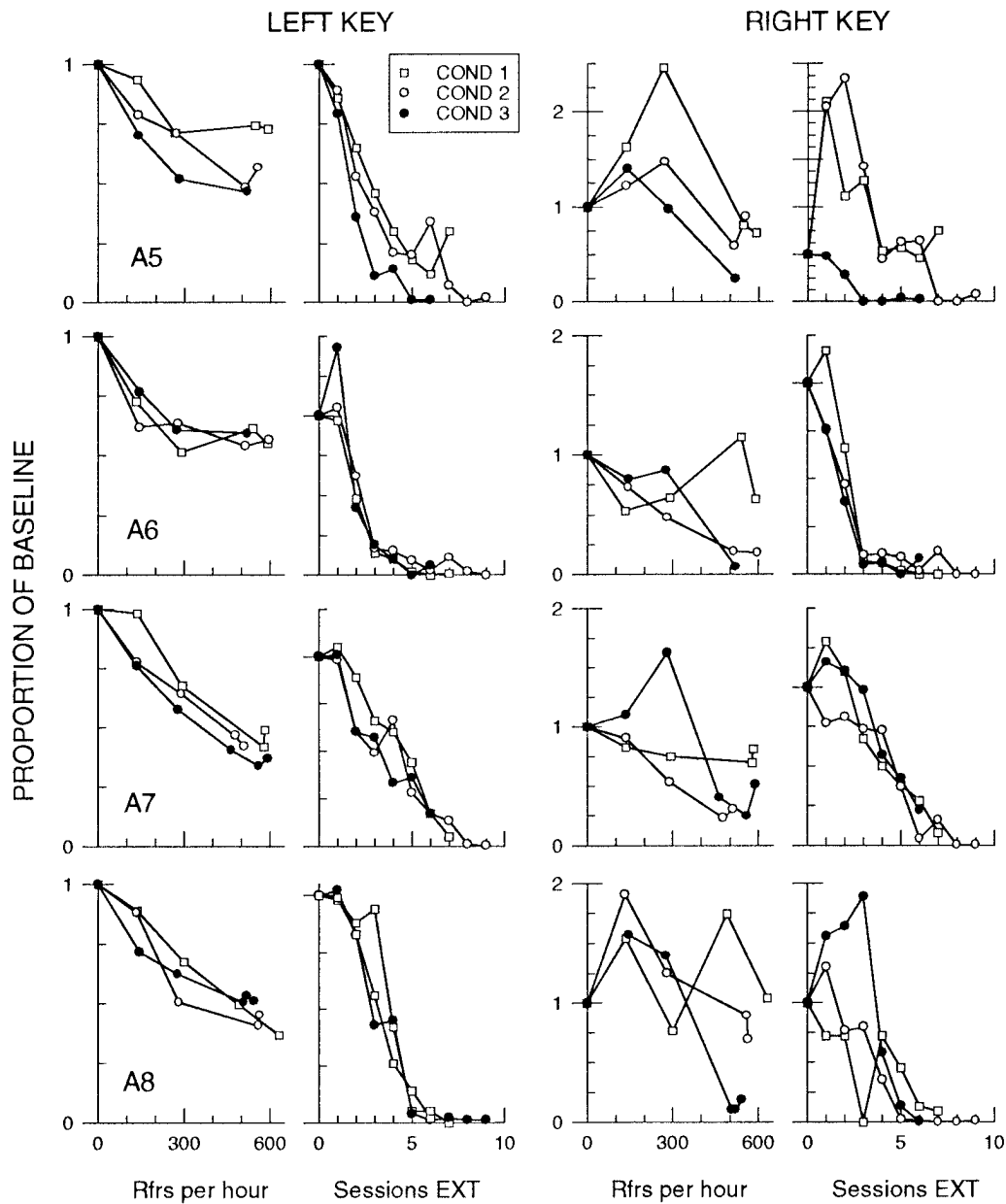
Fig. 1. Response rate in Component 1, expressed as a proportion of the mean rate from the 10 immediately preceding baseline sessions, as a function of the rate of response-independent reinforcement delivered during inter-component blackouts or number of sessions of extinction. Data for different conditions are represented by different symbols, and each row contains a different bird's data. The leftmost two columns give data for the left key with response-independent food and extinction as disruptors. The rightmost two columns give data for the right key. Note that all curves begin at 1.0 on the vertical axis, and that scales on the vertical axes vary. Data are from Conditions 1 through 3.
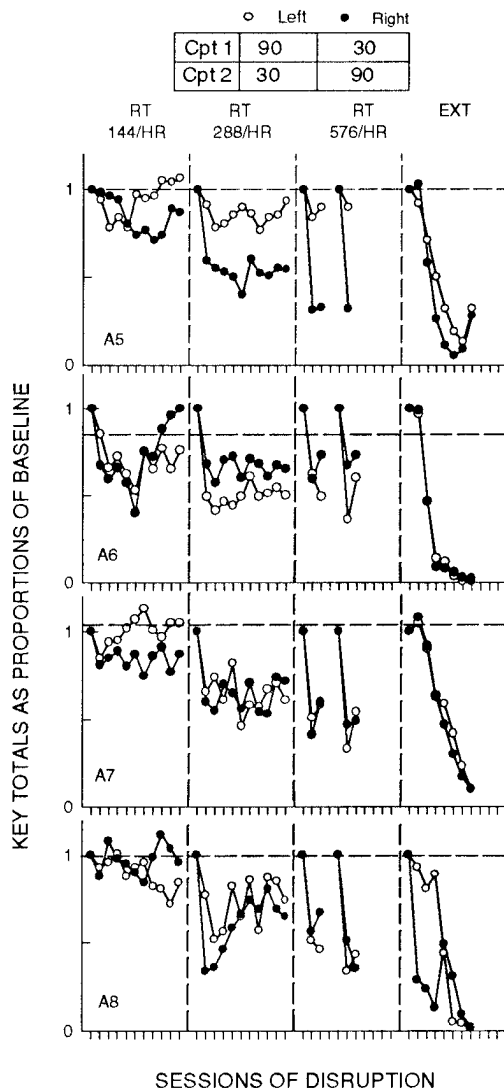
Fig. 2. Response-rate totals for left and right keys in Condition 1, summed across components and expressed as proportions of totals in baseline. Open circles give data from the left key, and filled circles give data from the right key. The matrix at the top gives arranged reinforcers per hour for each key and component. Different columns give data for extinction or RT food during blackouts, and different rows give data from different birds. Response rates are plotted over sessions within a resistance test. Note that the response-independent food test with 576 reinforcers per hour was conducted twice.

when high rates were used or when extinction was introduced. Overall, the analyses for Conditions 2 and 3 are consistent with the between-condition analysis in Figure 1 in that there appears to be no systematic ordering as a function of key locations in terms of resis-

tance to change. Over subjects, no consistent effect of location–reinforcer relations was evident for any of the disruptor conditions. A further analysis, which summarizes data from all three conditions in Series 1, will be presented later.

Series 2: Effects of the Stimulus–Reinforcer Contingency

In Series 2, the issue was whether responding in a component with a large reinforcer total (summed over locations) would resist the effects of response-independent food more than that in a component with a smaller reinforcement total. Over Conditions 3 through 5, the arranged ratios of reinforcer totals were varied over more than 1 log unit: 0 in Condition 3, −0.6 in Condition 4, and +0.48 in Condition 5. Response totals were calculated for each component by summing response rates over the two keys in baseline conditions and in the presence of disruptors. Figure 4 shows proportion of baseline response rate over sessions for each disruptor used in Condition 3. Noncontingent food reduced response totals in the two components to a similar extent, as would be expected from the equal reinforcer totals for components. Similarly, extinction proceeded at more or less the same rate in the two components. Data from Condition 4, in which unequal reinforcer totals were scheduled for components, are treated similarly in Figure 5. Response-independent food again reduced responding in both components, with one exception (Bird A5 with 288 RT food deliveries per hour). In every case, responding in Component 1, with the leaner VI schedule, was reduced more than that in Component 2, the reinforcement-rich component.

In Condition 4, the component stimulus–reinforcer relation was the same as the location–reinforcer relation, and the result may seem to be ambiguous as to whether differential resistance was the result of differences in reinforcement between components or differences between key locations. However, the lack of control over relative resistance by location–reinforcer contingencies, described above, indicates that these results are better interpreted in terms of contingencies between component stimuli and reinforcers.

In Condition 5, reinforcer totals again differed between components, but in this con-

CONDITION 2		o Left	● Right
	Cpt 1	90	30
	Cpt 2	0	120

CONDITION 3 (A7 & A8)		o Left	● Right
	Cpt 1	90	30
	Cpt 2	120	0

OR 3a (A5 &A6)		o Left	● Right
	Cpt 1	90	30
	Cpt 2	90	30

RT   RT   RT   EXT   RT   RT   RT   EXT
144/HR   288/HR   576/HR   144/HR   288/HR   576/HR

KEY TOTALS AS PROPORTIONS OF BASELINE

A5

A6

A7

A8

B 4 8   B 4 8   B B   B 4 8   B 4 8   B 4 8   B B B   B 4 8
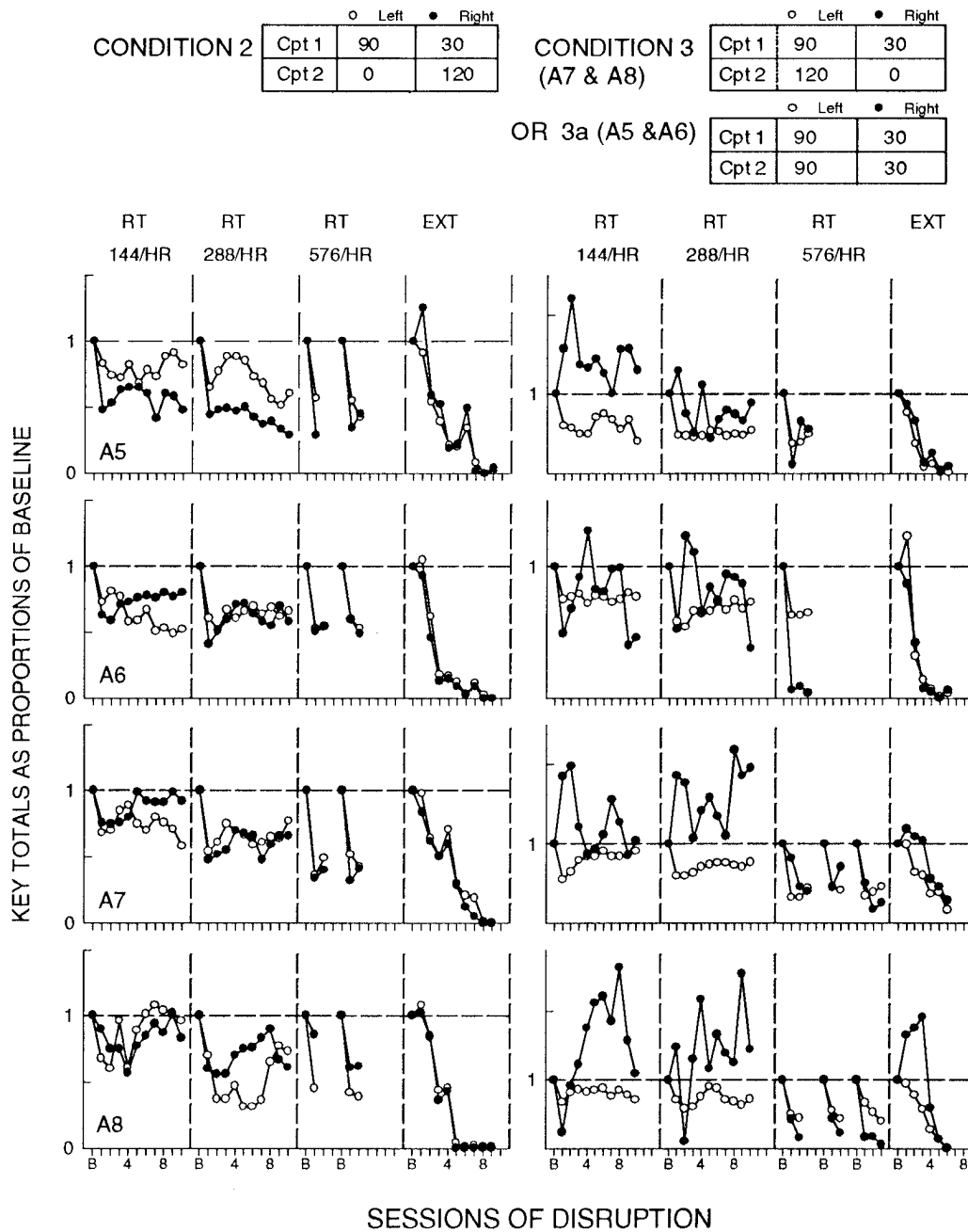
SESSIONS OF DISRUPTION

Fig. 3. Response-rate totals for left and right keys, summed across components and expressed as proportions of totals in baseline. Open circles give data from the left key, and filled circles give data from the right key. The left part gives data from Condition 2, and the right part gives data from Condition 3 (or 3a for Birds A5 and A6). Matrices at the top give arranged reinforcers per hour for each key and component. Different columns give data for extinction or RT food during blackouts, and different rows give data from different birds. Response rates are plotted over sessions within a resistance test. Note that the response-independent food test with 576 reinforcers per hour was sometimes conducted more than once.

	Left	Right
A7 & A8 ○ Cpt 1	90	30
● Cpt 2	120	0

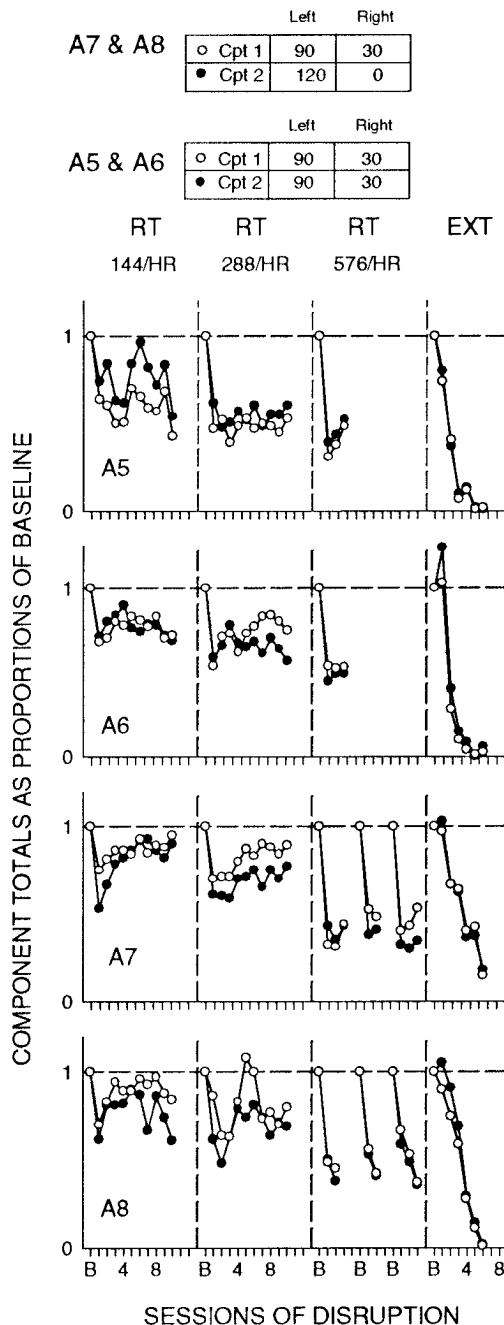|	Left	Right
A5 & A6 ○ Cpt 1	90	30
● Cpt 2	90	30

Fig. 4. Response-rate totals for Components 1 (open circles) and 2 (filled circles), summed across keys and expressed as proportions of totals in baseline, in Condition 3 (or 3a for Birds A5 and A6). Matrices at the top give arranged reinforcers per hour for each key and component. Each column gives data from a different resistance test, and each row gives data from a different bird. Response rates are plotted over sessions within a resistance test.

dition the total was greater in Component 1. Figure 6 shows again that total responding in the reinforcement-rich component was more resistant to noncontingent food than that in the leaner component. Total responding in the presence of each disruptor, as a proportion of total responding in baseline for the same component, is plotted over sessions of disruption for each of the two components. Again, filled circles represent data from the reinforcement-rich component and undergo consistently smaller reductions when noncontingent food was presented than did totals in the leaner component. Thus, Conditions 4 and 5 reversed the relation between components in terms of total reinforcement, and a corresponding reversal was observed in resistance to change.

Quantitative Analysis

The results obtained from each disruptor in each condition can be summarized by resistance ratios derived from the reductions in responding produced by response-independent food or extinction. For example, resistance ratios for key locations represent the reduction in responding (collapsed over components) for the left key divided by that for the right key, averaged over all of the tests using noncontingent food as the disruptor. This measure was computed by calculating total response rate for each key (summed over components) during baseline and disruptor conditions. Data from all baseline determinations in each condition were averaged, as were those from each determination with a given scheduled rate of noncontingent food in blackouts. Logarithms of response rates in baseline and during each disruptor were then related to the rate of RT food in blackouts, using linear regression, and the reciprocals of ratios of regression-line slopes were then calculated to yield resistance ratios for key locations. Analogous computations were performed for resistance ratios over Components 1 and 2, using responding summed over keys within each component in baseline and disruption conditions. These computations were all conducted using the data given in the Appendix.

When resistance ratios are plotted as a function of ratios of reinforcer totals, their sensitivity to reinforcer ratios can be assessed. Figure 7 gives this analysis for both of the ma-
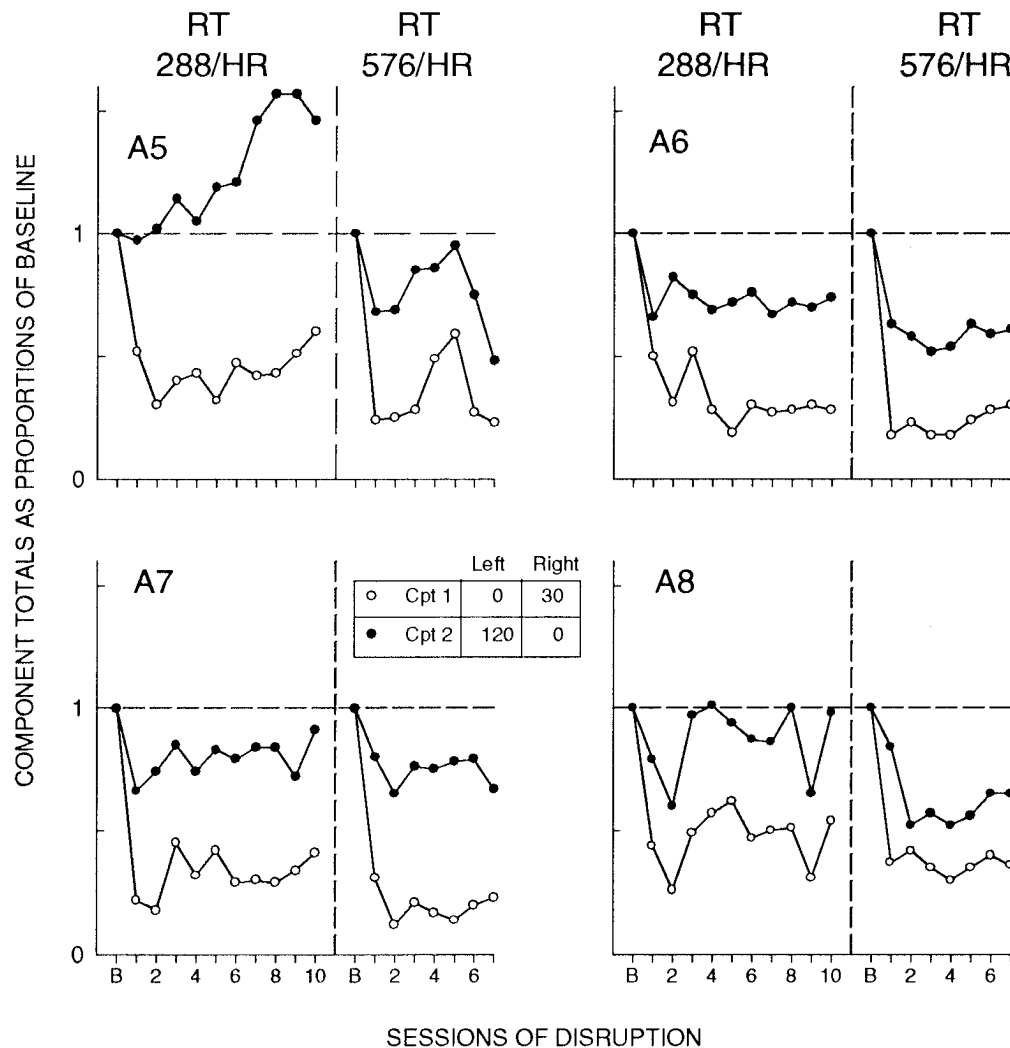
Fig. 5.   Response-rate totals for Components 1 (open circles) and 2 (filled circles), summed across keys and expressed as proportions of totals in baseline, in Condition 4. The matrix near the middle of the panels gives arranged reinforcers per hour for each key and component. Each panel gives data from a different bird. Columns within each panel give data from different resistance tests. Response rates are plotted over sessions within a resistance test.

nipulations used in the experiment. The upper panels of Figure 7 confirm the main results from each series. The right panel shows that resistance of responding in a component to the effects of RT food in blackouts was affected by the total reinforcement obtained in the component. Log resistance ratios were a positive function of log reinforcer ratios, and the relation was described by a straight line with a slope of 0.81. The standard error of the slope indicates that, even though 4 different subjects' data are analyzed together, the sensitivity of resistance ratios to differen-

tial stimulus–reinforcer contingencies was well estimated.

By contrast, the upper left panel shows that relative resistance of responding on a key was not affected by total reinforcers obtained by responding on that key. Log resistance ratios were not systematically related to log ratios of reinforcer totals, in that the slope of the regression line (0.14) was smaller than its standard error (0.18). The only data that were consistent with a positive relation between relative resistance and relative reinforcement for location were those from Condition 4. In
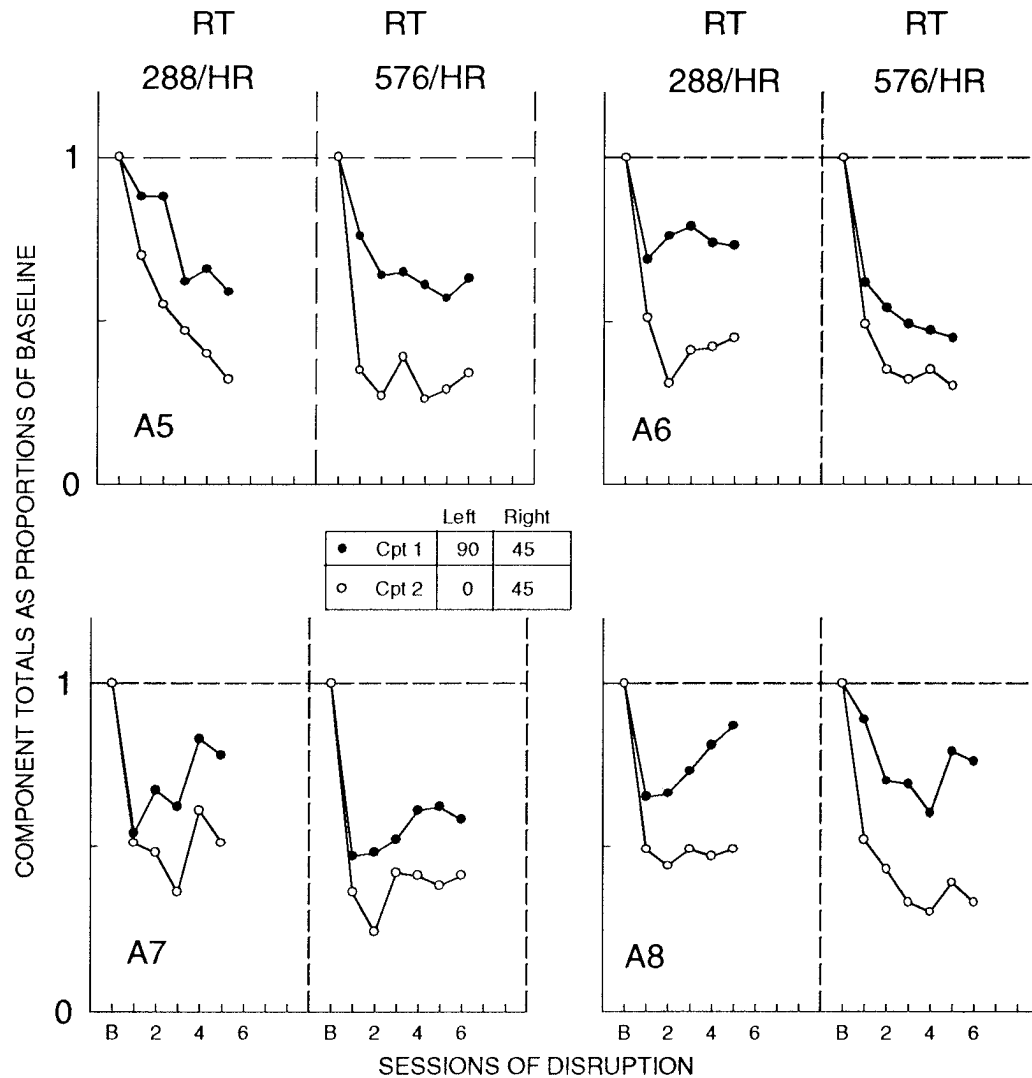
Fig. 6. Response-rate totals for Components 1 (open circles) and 2 (filled circles), summed across keys and expressed as proportions of totals in baseline, in Condition 5. The matrix near the middle gives arranged reinforcers per hour for each key and component. Each panel gives data from a different bird. Columns within each panel give data from different resistance tests. Response rates are plotted over sessions within a resistance test.

this condition, multiple-schedule components were differentiated both by stimulus and by location (see Table 1), and ratios of component totals were the same as ratios of location totals. Therefore the high and tightly clustered resistance ratios for this condition (the uppermost four data points at the log reinforcer ratio of 0.6) may owe to either the reinforcer ratio for locations or that for components. The remaining data in the left panel suggest that those four data points were not part of a general function relating relative re-

sistance to relative reinforcement for key locations.

The lower panels of Figure 7 show log resistance ratios for locations only. Data from Conditions 4 and 5 were omitted, leaving only conditions in which the ratio of reinforcer totals for components was constant (1.0) and that for locations was varied. The left panel gives data obtained using response-independent food as the disruptor, and the right panel gives log resistance ratios obtained using extinction. Extinction data were
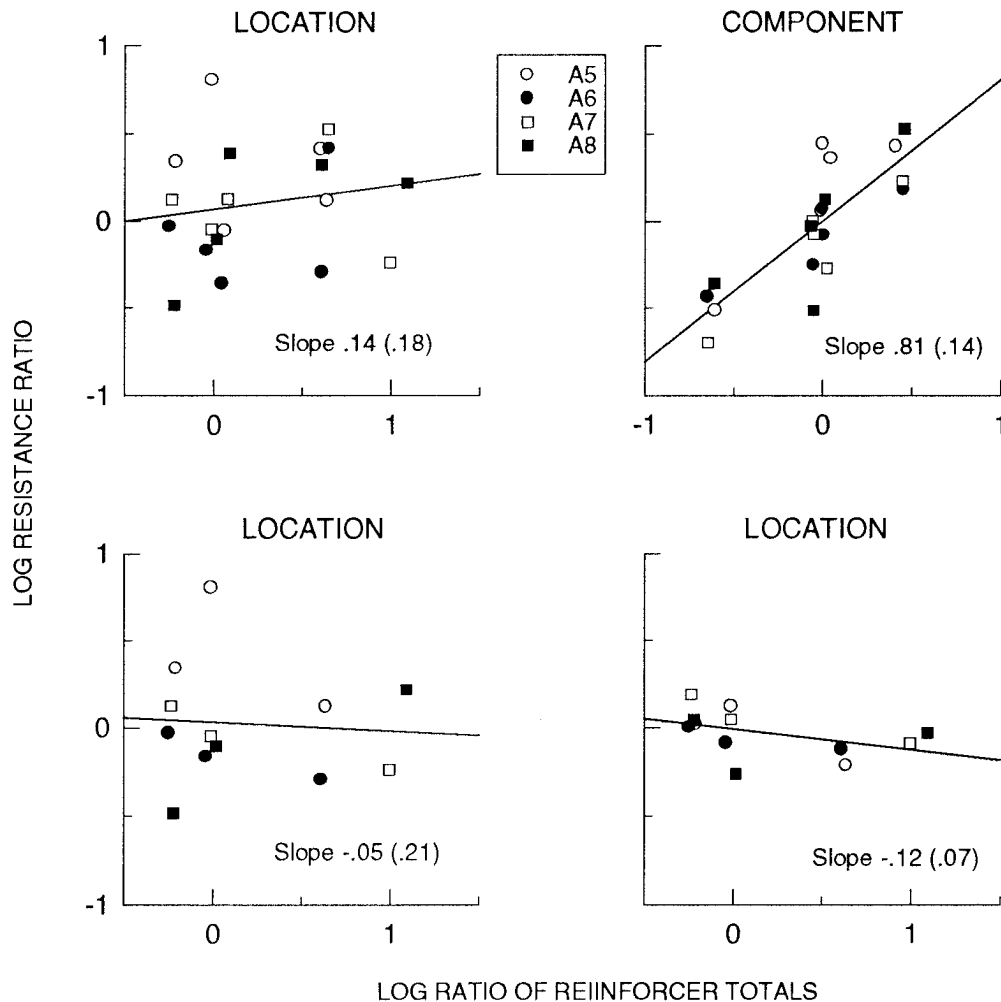
Fig. 7. Log resistance ratios for components (Component 1:Component 2) (upper right panel only) or key locations (left:right) (remaining panels), plotted as a function of the corresponding log of the ratio of reinforcer totals for components or keys, respectively. The lower right panel gives log resistance ratios obtained using extinction as the disruptor, and all others give data obtained using response-independent food. In all four panels, data from each of the 4 birds are represented by different symbols. Solid lines are least squares regression lines fitted to all of the data points shown in the panel, and their slopes are also given. Standard errors of slopes are given in parentheses. The upper row gives data from all conditions, and the lower row gives data from Conditions 1 through 3.

analyzed by regression of log response rate on the first and subsequent sessions of extinction versus number of sessions (cf. Nevin et al., 1987), not including data from any sessions conducted after response rate had reached zero in either component. Resistance ratios were calculated as before. Only the data obtained using extinction suggest a relation between relative resistance and relative reinforcement. The negative slope suggests that resistance to extinction was perhaps greater for the location with the lower total

of reinforcement, although the result is not entirely compelling because the slope is not much greater than its standard error, and the negative relation is apparent for only 3 of the 4 birds.

Finally, the steep function relating resistance ratios for components to component reinforcer ratios (upper right panel of Figure 7) was rather surprising because shallower functions are usually found (Nevin, 1992b). We explored this relation further by analyzing responding over successive 15-s subinter-
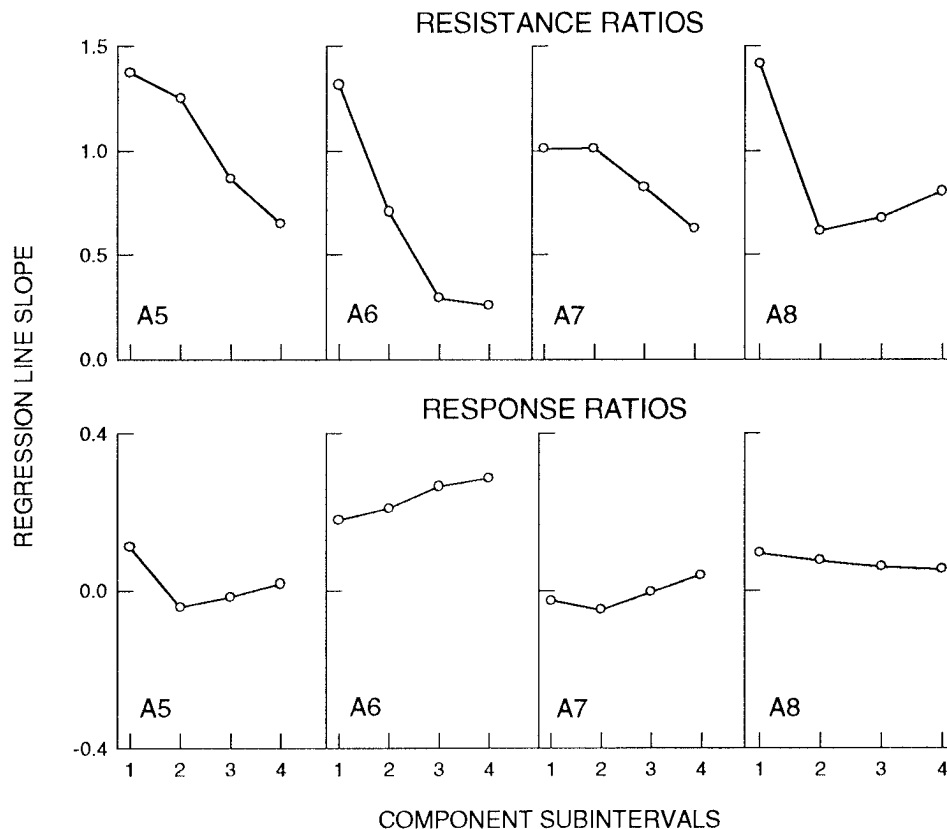
Fig. 8. Slopes of regression lines relating log resistance ratios to log reinforcer ratios (upper panel) or log response ratios in baseline to log reinforcer ratios (lower panel). Both analyses used ratios of totals in components. Slopes are shown for four successive subintervals of components in Conditions 4 and 5.

vals of components in Conditions 4 and 5. Specifically, log resistance ratios were calculated for each subinterval and were plotted as a function of log reinforcer ratios in Conditions 4 and 5, as in the upper right panel of Figure 7. Slopes of the regression lines relating resistance ratios to reinforcer ratios were found to vary systematically over subintervals. Figure 8 (upper row) summarizes these changes by showing the regression-line slopes for each component subinterval. All 4 subjects showed a particularly strong relation between relative resistance and relative reinforcement during the first subinterval (regression line slopes were all greater than or equal to 1.0). In later subintervals, the slopes were lower with one exception (Bird A7 in the second subinterval). Overall, a decreasing function relating regression-line slopes to time spent in components is apparent. The lower row in Figure 8 gives regres-

sion-line slopes for log ratios of baseline response totals in components versus log ratios of reinforcer totals. These slopes were estimated using data averaged over baseline determinations in Conditions 4 and 5, and did not use data from resistance tests. These slopes were clearly not a function of time spent in a component, and except for Bird A6 were overall close to zero. Thus, sensitivity of resistance ratios to reinforcer ratios was a decreasing function of time spent in a component, as has often been reported when sensitivity of response-rate ratios is studied using the generalized matching relation (e.g., McLean & White, 1981), although sensitivity of baseline response-rate ratios was constant in our data. Presumably, the effect on generalized matching slopes for response rate was not replicated in this procedure because of the 30-s blackouts between components, which were not used in McLean and White's study.
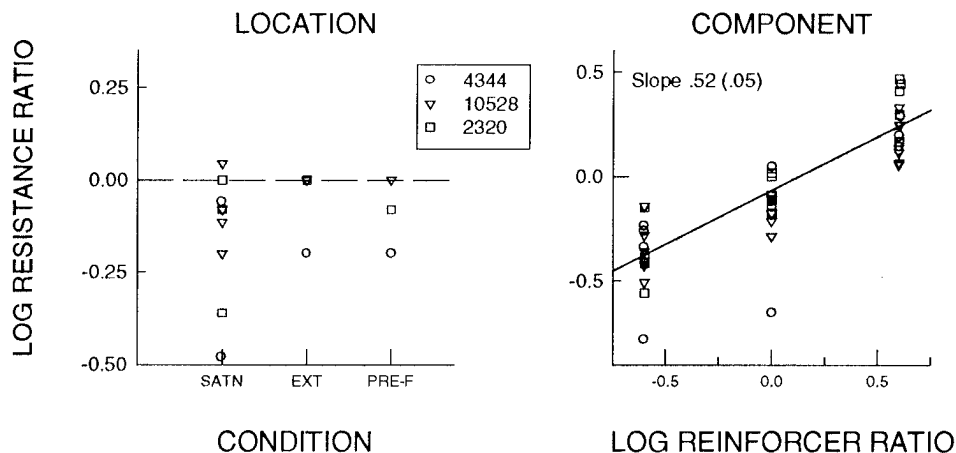
Fig. 9. Log resistance ratios for key locations (left panel) and components (right panel) in Experiment 2 of Nevin et al. (1990). The left panel gives data for key locations in each of three resistance tests. The right panel gives log resistance ratios for components in different pairwise combinations, plotted as a function of log reinforcer ratio for components. Data from each of the 3 birds are represented by different symbols. The solid line in the right panel is a least squares regression line fitted to all data points with nonzero log reinforcer ratio values. The slope of this line is given, with its standard error in parentheses.

DISCUSSION

The arguments given above, and our failure to find an effect of the location–reinforcer correlation on resistance to change, clearly challenge Nevin's (1992b) use of location–reinforcer contingencies to integrate results from a number of related experiments, as well as the argument for such an effect in Experiment 2 of Nevin et al. (1990). We address the latter issue first.

Nevin et al. (1990) employed a three-component multiple schedule with 45 reinforcers per hour on the left and 15 per hour on the right in Component A, 0 per hour on the left and 15 per hour on the right in Component B, and 0 per hour on the left and 60 per hour on the right in Component C. When they compared resistance to change on the left and right keys in Component A, they concluded that responding on the right key was generally more resistant to change. This was contrary to expectations based on the notion that resistance depends solely on component stimulus–reinforcer relations, according to which resistance to change should have been similar on the two keys in Component A. We reanalyzed these data using response rates summed for key locations and for components, as we have done in the foregoing analyses. The right panel of Figure 9 gives log resistance ratios for components, plotted as a

function of log ratios of reinforcers for components, using component pairs B versus C (a log reinforcer ratio of −0.6), A versus C (a log ratio of 0), and A versus B (a log ratio of +0.6). A regression line (fitted to ratios for A vs. B and B vs. C) had a slope of 0.52, confirming the effect of component stimulus–reinforcer contingencies on resistance to change when response rates were summed across keys. The left panel of Figure 9 gives log resistance ratios for locations, calculated using responding for each key summed over components, in each of three resistance tests. Across tests, log resistance ratios were generally negative, confirming the small but consistent differences in resistance to change between key locations that was originally reported by Nevin et al. (1990).

Nevin (1992b) argued that the difference between keys could be explained by the fact that the right key was correlated with a total of 90 reinforcers per hour across all three components, whereas the left key was correlated with only 45 reinforcers per hour, a difference that should have made right-key responding more resistant to change. However, the left:right reinforcer ratio was not varied, and the difference could also be explained if there was a right-key bias, despite efforts during preliminary training to prevent this. This suggested bias is consistent with the fact that

most of the data points with the log reinforcer ratio of zero show that resistance was greater in Component C than in Component A. This difference could result from the fact that most of the Component A pecks occurred on the left key. Moreover, Components 1 and 2 in our Condition 2 replicate Components A and C of Nevin et al. (1990) with richer schedules, and there was no evidence of consistent differences in resistance to change between keys (see Figure 3). Thus, evidence for a location effect arose from a post hoc analysis of an experiment that was not designed to evaluate it, whereas there was no supporting evidence from an experiment that was explicitly designed to evaluate it. We conclude that there is no consistent evidence of a positive relation between resistance to change and the location–reinforcer relation.

Why might the relations between color stimuli and reinforcers affect resistance to change in multiple schedules, whereas those between location stimuli and reinforcers in concurrent schedules do not? On the face of it, key locations cannot logically enter into the stimulus–reinforcer contingency ratio used by Nevin (1992b) to characterize determiners of resistance to change. Because both location stimuli (i.e., both keys) are constantly present throughout a component, reinforcers cannot be differentially correlated with the presence of one or the other of the two stimuli. However, it might be argued that a Pavlovian stimulus–reinforcer contingency exists by virtue of the location of the animal's responding. That is, when the subject is responding on, say, the left key, it may be said that it is more distinctly in the presence of the left-key stimulus than the right-key stimulus. If the left key also delivers more reinforcers than the right, then a stimulus–reinforcer contingency relation might be said to exist. This would be a stimulus–reinforcer relation quite different from that found in multiple schedules, however. In multiple schedules, stimuli signal different rates of reinforcement. If we take account of the time spent at each of two key locations by subjects in concurrent schedules, the different component stimuli (locations) are correlated with *equal* rates of reinforcement. Because subjects approximately match relative time spent on an alternative to relative reinforcement at that alternative, they equalize local rates of reinforcement on the two components (Rachlin, 1973; Vaughan, 1981). Thus, the relations between reinforcement and concurrent-schedule components, taking account of the subject's differential allocation of time between response locations, are equal. If relative resistance to change is a function of contingencies between stimuli and local rates of reinforcement, then location stimuli for concurrent alternatives would acquire equal resistance to change regardless of relative reinforcement overall, as we found.

The integrative model proposed by Nevin (1992b) employed the location–reinforcer relation to account for resistance to change in a number of experiments involving chained and serial schedules arranged on separate keys (Nevin, 1984; Nevin, Mandell, & Yarensky, 1981; Nevin et al., 1987). If the location–reinforcer relation is ineffective, these results must be explained in other ways. One way is to emphasise temporal (rather than spatial) relations between stimuli and reinforcers in serial schedules. A regular sequence of stimuli may be treated as a serial compound stimulus that defines the stimulus context correlated with reinforcement, in the same way as the stimulus that accompanies a component in a conventional multiple schedule. Thus, for example, a serial schedule defined by the stimuli white-on-the-left (correlated with 36 reinforcers per hour) followed by blue-on-the-left (correlated with 180 reinforcers per hour) can be viewed as a serial compound stimulus in which location per se is irrelevant. That is, both white and blue could appear on any of several keys as long as the sequence is preserved, and the serial compound could be simply designated W36-B180. The resistance of a member of the sequence (say, responding in the white component) can be viewed as depending on the entire serial compound in which it is embedded, independently of location. Specifically, the sequence W36-B180 generates greater resistance in white than another sequence, W36-G0 arranged on the right key, not because of the additional reinforcers obtained at the left key location in the second component, but because white on the left is always followed by additional reinforcement whereas white on the right is not. Indeed, this interpretation readily deals with the results from a study by Nevin et al. (1987), who used conditions with W36-B180

on the left and center keys and W36-G0 on the right and center keys. Greater resistance to change was found for the white component of the serial schedule that began on the left key than for the white component that began on the right. Nevin (1992b) evidently failed to note that location per se cannot account for this result because the reinforcer differential between the two sequences derives from the second component, which was located on the center key in both cases.

However, the serial compound cannot be the sole determiner of resistance to change. For example, Nevin et al. (1981) compared resistance to change in the initial and terminal links of multiple chained schedules. In one condition, the schedules were R0-G90(10) on the left key and Y0-B90(2) on the right key, where the numbers in parentheses indicate reinforcer duration. In both of these chains, and in seven other multiple chained schedule conditions reported in their article, initial-link responding was less resistant to change than was terminal-link responding. Because both initial and terminal links were equally embedded in their serial compounds, we must also consider the reinforcers correlated with the individual components that comprise the sequence. One way to do this is to express resistance ratios as a joint function of the ratios of reinforcers in those components and the ratios of reinforcers correlated with the two distinctively signaled sequences within which the components appear. This is exactly what Nevin's (1992b) integrative model accomplished, using location as one of the joint determiners of resistance. Coupled with the foregoing arguments, the failure to find location effects in the present study suggests that "location" be replaced by "serial compound stimulus" in the calculation of the contingency ratio that Nevin (1992b) employed to unify the results of all his experiments on resistance to change. However, neither the present study nor the earlier experiments were designed to explore the properties of serial compound stimuli, and further empirical research is needed.

The results reported above, together with previous analyses by Nevin (1992b; see his Figure 2), suggest that in a two-component multiple schedule (in which serial compound stimuli are either undefined or identical, and

the contingency ratio is simply the ratio of the component reinforcer rates), the ratio of the resistance to change in one schedule component to that in a second component is a power function of the ratio of reinforcers obtained in those components:

$$m_1/m_2 = (r_1/r_2)^b, \qquad (1)$$

where m_1/m_2 represents the resistance ratio, r_1/r_2 represents the reinforcer ratio, and b represents the sensitivity of the resistance ratio to the reinforcer ratio. Our Figure 7 (upper right panel) is a logarithmic form of Equation 1, and we obtained an estimate of 0.81 for b when the resistance ratios of sums of left-key and right-key responses were related to component reinforcer ratios. Our results suggest that the resistance of the sum of two responses is functionally similar to the resistance of a single response in Nevin's analyses. However, our value of b is substantially greater than Nevin's (1992b) value of about 0.35. One reason for this discrepancy may be that Nevin's estimate was based on a combination of data from many separate experiments, and there was a good deal of unsystematic variation within his summary plot (see Nevin, 1992b, Figure 5). The present value may fall within the range of variation in his analyses. Alternatively, it may be that the resistance of the within-component sum of two differentially reinforced responses is more sensitive to the stimulus–reinforcer relation than is the resistance of a single response. This conjecture is supported by our reanalysis of the data of Nevin et al. (1990, Experiment 2; see our Figure 9, right panel), where the value of b is 0.52, which is also greater than Nevin's (1992b) estimated value.

Studies of maintained response rates in multiple schedules have often used the generalized matching law to summarize their results. The standard expression is

$$B_1/B_2 = c(r_1/r_2)^a, \qquad (2)$$

where B_1 and B_2 represent response rates and r_1 and r_2 represent reinforcer rates in Components 1 and 2, respectively. The parameter a represents the sensitivity of response-rate ratios to reinforcer-rate ratios, and the parameter c represents a bias toward responding in one or the other component (e.g., a color preference) that is independent of reinforce-

ment. Multiplying Equations 1 and 2, we obtain

$$\frac{m_1 B_1}{m_2 B_2} = \left(\frac{r_1}{r_2}\right)^{a+b}. \qquad (3)$$

In the metaphor proposed by Nevin et al. (1983), behavioral momentum is given by the product of resistance to change (*m,* the mass-like aspect of behavior that is evidenced by its resistance to change) and baseline response rate (*B,* the metaphorical equivalent of velocity). To achieve a comprehensive account of behavioral momentum, we need to understand the determiners of both *a* and *b.* Research on the generalized matching law for multiple-schedule performance has identified several determiners of *a* (for review, see Davison & McCarthy, 1988; McSweeney, Farmer, Dougan, & Whipple, 1986). It now appears that a comparable program of research will be needed to identify the determiners of *b.*

Our present results and those of Nevin (1992a) offer a beginning to that program. Nevin used multiple schedules with 2-s or 120-s timeouts separating two components with different rates of reinforcement. His data indicate that values for *a* were much lower with the longer timeouts but values for *b* were about the same, suggesting that intercomponent blackouts do not have the same effect on parameters *a* and *b.* Another way to examine the relations between *a* and *b* is to compare changes in these measures over subintervals of multiple-schedule components. Values for *a* in subintervals of components usually decrease as components progress (e.g., McLean & White, 1981), and our analysis across component subintervals (Figure 8) demonstrates that *b* undergoes similar changes within components. However, in the present data, values for *a* were consistently close to zero and did not change over subintervals. Presumably, the 30-s blackout between components in this study (but not in that of McLean and White) reduced *a* to zero and eliminated effects of time spent in components. The orderly changes in *b* across subintervals, despite intercomponent blackouts, suggests that sensitivity of mass ratios and of velocity ratios may vary independently. It will be of considerable interest to ascertain whether *a* and *b* are similar, opposite, or independent functions of other variables such

as deprivation level, reinforcer amount or quality, and component duration.

Whatever the outcomes of such studies, the present research has refined the analysis of resistance to change in two-key multiple concurrent schedules by eliminating key location as a relevant variable. In addition, the application of resistance analyses has been extended by demonstrating that the sum of the rates of two concurrent responses is functionally similar to the rate of a single response in its dependence on the reinforcer rate correlated with a component stimulus. This is an important extension for two related reasons. First, it supports the notion that resistance to change is independent of response–reinforcer relations that determine the rate or allocation of responses within a schedule component. Second and more generally, it suggests that all responses maintained by a common reinforcer within a common stimulus context function as a single response class with respect to their resistance to change.

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APPENDIX

Average responses per minute (B), with standard deviations in parentheses, and average reinforcers per hour (R) for each key and each component. Rates were averaged over the last 10 sessions of each baseline determination, and over all sessions in each disruptor condition. Subscripts for B and R identify the key (left or right) and Component (1 or 2) concerned. The final column gives average reinforcers per hour during intercomponent blackouts (R_{BO})

Bird	Condition	B_{L1}	B_{R1}	B_{L2}	B_{R2}
A5	1	65.77 (3.12)	3.03 (1.71)	5.58 (4.33)	83.49 (4.97)
		61.62 (5.74)	4.94 (1.68)	5.26 (2.29)	67.75 (8.18)
		61.45 (3.63)	3.85 (3.13)	1.87 (0.21)	93.46 (5.50)
		44.87 (5.47)	2.80 (0.80)	10.17 (2.95)	28.01 (2.31)
		64.17 (5.32)	7.03 (3.13)	1.78 (0.90)	82.57 (3.22)
		47.70 (–)	5.68 (–)	11.59 (–)	22.97 (–)
		63.08 (6.12)	3.10 (1.66)	2.79 (1.05)	75.17 (4.96)
		44.91 (3.40)	7.62 (3.38)	10.95 (2.29)	33.75 (4.49)
		66.67 (4.36)	3.11 (1.80)	3.04 (0.97)	80.86 (4.76)
		23.90 (19.03)	5.29 (3.99)	3.03 (2.38)	19.93 (25.56)
	2	63.56 (1.73)	1.20 (0.24)	0.31 (0.29)	77.49 (3.63)
		50.06 (4.71)	1.46 (0.91)	0.45 (0.76)	42.76 (6.81)
		64.84 (5.22)	1.27 (0.24)	0.04 (0.06)	76.18 (5.03)
		45.99 (8.78)	1.87 (0.89)	0.12 (0.25)	30.56 (6.33)
		69.11 (5.36)	1.05 (0.20)	0.02 (0.05)	57.74 (8.38)
		39.28 (–)	0.94 (–)	0	16.17 (–)
		61.00 (4.72)	1.23 (0.25)	0	39.77 (3.84)
		29.67 (5.73)	0.73 (0.62)	0.07 (0.00)	15.57 (3.80)
		55.02 (6.21)	1.34 (0.45)	0	62.20 (8.83)
		16.08 (15.60)	2.26 (2.37)	0.28 (0.38)	21.11 (23.58)
	3	66.43 (5.36)	4.96 (1.44)	69.01 (6.98)	7.02 (3.00)
		30.96 (4.15)	1.20 (0.94)	25.71 (5.17)	4.03 (2.63)
		55.29 (3.71)	4.61 (1.56)	59.80 (5.26)	6.38 (1.56)
		38.83 (7.84)	6.43 (2.23)	29.14 (5.81)	9.61 (3.24)
		68.15 (6.40)	4.91 (1.39)	71.65 (5.79)	8.18 (1.65)
		35.32 (3.14)	4.81 (1.51)	33.15 (4.04)	5.48 (2.79)
		69.86 (6.33)	4.79 (0.70)	75.32 (6.42)	5.95 (1.55)
		16.34 (20.85)	1.30 (1.91)	16.38 (21.99)	2.34 (1.93)
	4	6.68 (4.47)	33.05 (7.35)	55.08 (9.79)	1.04 (1.01)
		4.42 (2.59)	13.02 (4.92)	70.13 (13.97)	0.83 (1.65)
		0.53 (0.40)	59.17 (5.53)	58.19 (5.51)	0.86 (0.71)
		0.74 (0.43)	19.25 (8.42)	43.66 (9.25)	0.71 (0.71)
	5	28.27 (3.96)	10.98 (3.00)	9.06 (4.72)	42.67 (6.31)
		7.91 (6.79)	20.67 (11.48)	6.50 (7.36)	18.87 (4.08)
		32.74 (6.59)	9.38 (3.17)	4.04 (2.41)	54.81 (3.45)
		14.82 (5.29)	12.28 (4.18)	1.84 (2.20)	16.75 (3.20)
A6	1	33.75 (3.95)	13.18 (1.92)	14.74 (2.51)	33.04 (3.39)
		24.50 (3.47)	7.02 (1.55)	9.23 (2.29)	26.28 (7.42)
		41.24 (4.12)	4.68 (1.84)	14.21 (1.97)	33.94 (5.03)
		25.26 (6.00)	5.36 (0.82)	5.60 (0.93)	20.22 (3.05)
		41.36 (3.43)	8.32 (2.33)	13.40 (1.87)	37.32 (1.80)
		22.81 (8.07)	5.27 (0.06)	3.55 (1.25)	26.81 (1.89)
		44.01 (4.46)	10.62 (2.57)	13.25 (3.90)	36.34 (2.90)
		22.61 (2.56)	6.81 (2.12)	5.74 (2.58)	24.10 (2.75)
		38.08 (3.30)	10.83 (2.10)	11.56 (2.19)	36.30 (4.04)
		9.32 (13.76)	3.06 (4.95)	3.06 (3.87)	8.58 (12.15)

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APPENDIX

(*Extended*)

when this was used as a resistance test. Data from conditions and resistance tests are listed in the order in which they were conducted. A dash (–) was entered for standard deviations if only one session's data were collected in a test. When extinction was used as a test, this is indicated by zeros in the reinforcer-rate columns.

R_{L1}	R_{R1}	R_{L2}	R_{R2}	R_{B0}
86.29 (6.36)	20.96 (8.54)	18.68 (3.60)	84.28 (6.58)	0
82.42 (8.16)	18.25 (7.42)	19.96 (6.52)	82.06 (9.56)	136.30 (17.3)
80.98 (9.30)	17.33 (5.87)	21.81 (6.87)	85.90 (7.99)	0
84.20 (9.59)	10.78 (3.00)	23.56 (9.25)	59.89 (0.45)	591.04 (37.76)
83.75 (5.88)	24.46 (6.39)	18.33 (6.91)	87.09 (8.70)	0
82.01 (–)	12.95 (–)	30.43 (–)	73.91 (–)	547.57 (–)
83.84 (4.96)	19.13 (5.19)	18.32 (8.07)	86.60 (7.76)	0
84.71 (6.82)	18.28 (8.76)	22.42 (5.83)	69.38 (8.75)	267.59 (39.92)
89.01 (6.21)	19.65 (6.31)	20.09 (6.70)	87.66 (6.90)	0
0	0	0	0	0
85.25 (9.14)	18.72 (5.97)	0	115.83 (7.28)	0
83.72 (9.35)	16.93 (7.57)	0	110.12 (10.64)	138.79 (25.14)
79.40 (5.18)	22.17 (8.68)	0	117.79 (10.38)	0
78.43 (8.72)	20.40 (6.99)	0	107.68 (5.03)	272.45 (45.73)
87.73 (5.95)	21.42 (7.91)	0	119.70 (8.80)	0
82.01 (–)	12.95 (–)	0	99.64 (–)	556.10 (–)
86.12 (8.78)	18.29 (8.23)	0	114.37 (5.27)	0
82.34 (19.82)	15.16 (3.33)	0	92.74 (16.41)	514.44 (23.09)
82.21 (9.21)	21.76 (5.93)	0	115.32 (4.56)	0
0	0	0	0	0
78.11 (9.56)	15.56 (6.93)	79.74 (5.55)	19.96 (5.56)	0
83.25 (2.14)	8.63 (7.48)	72.52 (8.65)	7.10 (6.50)	519.81 (12.52)
84.09 (7.62)	15.61 (3.71)	84.32 (7.26)	19.13 (5.56)	0
81.65 (10.22)	20.41 (6.19)	70.63 (7.53)	20.69 (6.18)	141.56 (20.38)
81.66 (10.53)	20.41 (5.87)	78.29 (3.54)	18.61 (5.88)	0
77.65 (9.62)	15.55 (6.53)	77.07 (10.09)	13.77 (5.31)	283.69 (24.97)
81.54 (9.19)	19.10 (8.05)	81.24 (8.45)	21.31 (7.37)	0
0	0	0	0	0
0	26.60 (5.66)	113.89 (5.04)	0	0
0	16.63 (3.03)	114.38 (6.92)	0	256.03 (22.34)
0	30.80 (6.91)	116.29 (4.68)	0	0
0	24.52 (6.79)	112.53 (6.62)	0	541.92 (57.45)
75.89 (7.63)	24.72 (6.82)	0	37.56 (5.09)	0
28.78 (29.25)	25.80 (10.49)	0	31.20 (3.77)	286.49 (14.67)
74.70 (8.49)	27.38 (6.96)	0	41.39 (4.50)	0
51.37 (14.74)	30.60 (6.15)	0	37.83 (4.18)	571.15 (67.05)
75.52 (8.57)	25.60 (3.31)	27.85 (8.62)	76.07 (5.99)	0
76.10 (7.86)	20.37 (8.90)	25.05 (5.40)	69.52 (8.72)	133.33 (34.7)
82.17 (6.61)	14.72 (5.15)	25.18 (6.75)	77.31 (9.14)	0
71.27 (9.88)	23.76 (3.29)	19.39 (3.00)	73.26 (6.28)	539.13 (0)
83.57 (9.52)	21.34 (5.68)	28.79 (4.41)	78.52 (10.13)	0
59.48 (6.16)	14.86 (2.97)	12.90 (0.07)	77.44 (6.48)	591.04 (113.7)
82.30 (9.22)	23.10 (6.65)	22.90 (6.58)	71.22 (8.17)	0
72.86 (7.91)	20.27 (7.67)	15.96 (8.72)	74.91 (9.74)	290.68 (38.96)
80.89 (9.85)	22.63 (5.88)	26.15 (8.35)	79.21 (6.02)	0
0	0	0	0	0

APPENDIX

(*Continued*)

Bird	Condition	B_{L1}	B_{R1}	B_{L2}	B_{R2}
	2	44.62 (1.83)	9.64 (1.88)	0.20 (0.19)	46.23 (2.45)
		27.64 (5.29)	7.03 (3.08)	0.16 (0.13)	33.80 (2.30)
		43.59 (4.51)	8.02 (2.53)	0.02 (0.07)	53.71 (2.46)
		27.67 (2.20)	3.82 (1.75)	0.17 (0.15)	33.21 (5.59)
		43.34 (4.29)	13.29 (1.96)	0.17 (0.44)	53.41 (2.87)
		23.41 (0.56)	2.58 (0.71)	0	32.28 (1.93)
		36.88 (3.02)	13.97 (1.47)	0.09 (0.16)	45.99 (2.42)
		20.82 (1.87)	2.54 (1.15)	0.15 (0.00)	30.16 (3.70)
		36.20 (3.77)	13.87 (3.55)	0	51.41 (2.42)
		9.04 (12.84)	2.56 (3.55)	0.21 (0.30)	11.07 (16.43)
	3	31.66 (2.33)	9.00 (0.87)	31.52 (2.52)	10.90 (2.72)
		18.79 (0.94)	0.57 (0.07)	21.66 (0.76)	0.76 (0.46)
		36.55 (3.19)	9.71 (1.41)	36.66 (2.14)	10.29 (2.46)
		28.04 (1.00)	7.71 (2.53)	27.83 (1.89)	7.96 (3.84)
		34.57 (4.72)	7.67 (1.63)	35.82 (5.30)	10.63 (1.99)
		20.95 (1.97)	6.66 (2.73)	25.62 (2.81)	8.39 (3.38)
		30.34 (5.74)	12.50 (2.98)	33.07 (4.44)	9.91 (1.65)
		11.07 (16.47)	2.78 (3.71)	7.96 (13.16)	2.72 (3.95)
	4	1.17 (0.67)	21.13 (4.20)	49.00 (7.95)	0.42 (0.55)
		0.57 (0.88)	6.65 (1.54)	35.51 (2.38)	0.28 (0.52)
		0.48 (0.45)	24.99 (7.87)	50.42 (3.20)	0.14 (0.27)
		0.01 (0.03)	5.84 (1.27)	29.66 (2.20)	0.01 (0.03)
	5	37.82 (3.50)	11.66 (1.80)	2.30 (1.09)	31.87 (3.74)
		22.72 (3.76)	13.93 (2.35)	1.67 (2.13)	12.72 (2.47)
		43.43 (3.10)	8.27 (1.48)	0.30 (0.27)	36.38 (3.02)
		12.69 (0.51)	13.82 (3.45)	0.37 (0.20)	12.98 (2.61)
A7	1	74.85 (5.29)	26.80 (6.18)	29.36 (8.33)	93.32 (8.53)
		73.61 (4.89)	22.13 (6.02)	30.95 (6.97)	78.45 (8.43)
		73.72 (8.57)	26.48 (3.25)	21.80 (7.19)	88.81 (9.99)
		36.14 (6.38)	21.48 (4.44)	16.15 (1.72)	36.95 (10.58)
		74.66 (5.70)	28.80 (3.68)	27.91 (5.94)	90.93 (8.95)
		31.23 (9.32)	20.01 (1.63)	13.22 (5.71)	37.61 (0.09)
		73.05 (1.83)	27.92 (4.65)	30.11 (5.09)	88.93 (6.15)
		49.48 (7.72)	20.90 (3.35)	16.70 (4.07)	52.62 (7.16)
		76.92 (4.55)	30.36 (4.10)	26.95 (5.69)	89.91 (6.19)
		42.58 (27.87)	18.65 (13.31)	15.66 (8.09)	44.50 (31.88)
	2	82.15 (5.04)	24.03 (6.88)	6.27 (3.53)	102.20 (7.77)
		63.69 (7.97)	21.58 (8.71)	1.78 (1.11)	88.30 (7.13)
		79.18 (4.45)	22.89 (2.76)	2.17 (1.73)	112.95 (3.23)
		50.75 (6.25)	12.16 (3.60)	2.38 (1.70)	69.05 (9.83)
		90.30 (6.29)	17.68 (4.84)	1.32 (1.79)	121.00 (4.34)
		38.02 (8.45)	5.31 (1.33)	1.06 (0.26)	45.80 (5.22)
		93.38 (6.39)	17.27 (5.68)	2.26 (2.72)	122.04 (5.77)
		43.42 (5.13)	3.93 (1.23)	1.96 (0.72)	47.46 (7.48)
		88.30 (5.99)	22.17 (2.53)	1.39 (1.25)	135.76 (5.71)
		32.67 (29.41)	8.83 (7.91)	2.81 (2.08)	43.93 (41.95)
	3	89.17 (5.05)	14.39 (3.24)	97.02 (4.09)	10.13 (2.93)
		36.12 (3.50)	5.75 (2.34)	30.48 (10.76)	7.98 (3.58)
		76.73 (7.66)	16.43 (2.98)	92.72 (4.41)	5.37 (3.05)
		28.25 (1.87)	8.43 (3.74)	44.84 (2.75)	4.27 (0.11)
		80.93 (4.47)	19.05 (2.53)	98.51 (3.53)	1.01 (0.96)
		27.38 (2.57)	4.68 (3.04)	43.66 (7.81)	1.47 (0.68)
		83.95 (5.64)	13.89 (3.17)	101.67 (4.52)	0.72 (1.15)
		63.68 (12.83)	15.29 (3.64)	85.03 (9.10)	3.25 (4.08)
		89.77 (5.16)	10.04 (3.41)	98.13 (2.71)	0.59 (0.61)
		51.73 (5.55)	16.32 (3.91)	79.44 (8.63)	0.83 (1.17)
		92.16 (5.60)	15.23 (2.78)	102.59 (3.77)	0.61 (0.52)
		46.66 (27.26)	11.32 (5.95)	55.12 (28.89)	0.87 (0.52)

APPENDIX

(*Continued, Extended*)

R_{L1}	R_{R1}	R_{L2}	R_{R2}	R_{BO}
75.76 (6.85)	22.53 (7.12)	0	114.86 (6.32)	0
77.90 (8.91)	19.52 (9.11)	0	115.32 (3.24)	143.50 (17.87)
81.23 (7.25)	21.73 (7.98)	0	115.83 (7.60)	0
80.17 (9.49)	19.06 (4.24)	0	113.90 (7.12)	280.12 (41.98)
81.04 (6.62)	25.73 (7.38)	0	118.26 (9.23)	0
68.82 (0.00)	21.51 (0.00)	0	116.27 (3.40)	514.32 (11.55)
75.21 (8.89)	28.27 (6.96)	0	111.98 (6.47)	0
79.58 (3.44)	10.76 (3.10)	0	116.27 (3.40)	596.42 (57.01)
79.23 (8.81)	20.43 (10.62)	0	114.86 (7.09)	0
0	0	0	0	0
82.53 (9.84)	19.18 (9.23)	79.95 (7.58)	22.66 (9.33)	0
79.75 (7.07)	1.43 (2.48)	78.15 (9.42)	0	520.71 (49.79)
83.95 (9.60)	20.02 (5.94)	85.17 (6.76)	18.27 (7.39)	0
84.46 (5.33)	14.76 (7.79)	81.55 (10.43)	18.69 (8.82)	146.64 (22.62)
80.35 (4.34)	15.57 (5.51)	77.06 (7.70)	20.81 (6.29)	0
74.81 (7.94)	14.62 (6.17)	81.89 (6.50)	17.38 (8.56)	275.48 (45.97)
81.39 (8.29)	23.96 (8.63)	81.11 (7.28)	19.53 (5.59)	0
0	0	0	0	0
0	26.59 (4.51)	110.83 (21.14)	0	0
0	18.74 (8.32)	112.47 (7.14)	0	296.51 (38.22)
0	23.71 (8.53)	113.43 (7.67)	0	0
0	22.73 (6.27)	112.53 (6.62)	0	557.98 (63.02)
78.65 (4.87)	31.92 (7.04)	0	36.71 (5.09)	0
73.14 (9.88)	32.20 (4.94)	0	35.45 (7.72)	294.88 (45.56)
80.57 (8.72)	32.41 (7.04)	0	41.82 (4.70)	0
54.28 (5.88)	37.90 (3.54)	0	37.98 (5.56)	549.31 (85.16)
82.74 (9.09)	23.09 (6.88)	20.74 (6.06)	75.21 (10.43)	0
80.87 (8.56)	22.63 (6.53)	24.78 (8.84)	76.36 (6.67)	136.30 (21.62)
78.73 (9.56)	24.83 (7.92)	27.37 (8.08)	74.23 (8.41)	0
71.48 (3.06)	28.16 (3.06)	23.53 (3.08)	59.89 (0.15)	582.18 (87.4)
78.76 (9.58)	26.11 (8.27)	21.31 (10.13)	77.10 (7.56)	0
69.10 (6.81)	25.93 (6.37)	19.36 (9.38)	66.51 (10.10)	577.78 (118.37)
79.77 (9.54)	26.64 (9.37)	24.76 (7.76)	76.82 (7.46)	0
73.78 (13.77)	26.01 (5.53)	20.76 (7.49)	73.40 (9.06)	293.78 (43.42)
80.44 (8.60)	23.08 (7.88)	22.11 (7.60)	76.21 (8.47)	0
0	0	0	0	0
81.73 (8.47)	21.77 (8.08)	0	114.87 (8.12)	0
79.26 (13.46)	25.24 (5.81)	0	113.43 (7.32)	137.11 (21.35)
81.34 (9.29)	22.63 (6.17)	0	119.68 (6.36)	0
70.42 (6.18)	25.08 (6.24)	0	109.61 (8.24)	291.01 (23.47)
86.72 (4.89)	20.52 (8.32)	0	122.60 (7.86)	0
71.53 (9.92)	28.18 (3.35)	0	111.48 (3.38)	510.46 (28.73)
78.47 (6.97)	21.70 (6.87)	0	117.76 (8.46)	0
64.29 (0.32)	21.44 (6.17)	0	104.35 (0.00)	478.40 (16.59)
81.86 (10.13)	23.52 (6.59)	0	118.72 (7.52)	0
0	0	0	0	0
87.37 (9.35)	22.29 (6.11)	111.97 (5.62)	0	0
78.99 (16.16)	11.48 (2.52)	84.25 (11.51)	0	464.22 (17.66)
86.89 (7.60)	22.30 (6.44)	114.86 (6.36)	0	0
72.86 (6.06)	12.86 (6.06)	101.99 (3.33)	0	591.44 (37.81)
80.18 (10.77)	18.67 (7.80)	115.83 (7.60)	0	0
72.86 (4.32)	12.89 (8.63)	102.85 (11.84)	0	559.81 (47.49)
85.39 (9.72)	20.92 (7.16)	125.05 (9.15)	0	0
81.24 (6.72)	21.75 (7.76)	114.86 (7.10)	0	135.76 (25.95)
83.69 (9.40)	16.48 (4.96)	120.20 (9.74)	0	0
82.21 (9.15)	21.76 (5.89)	119.22 (8.64)	0	281.14 (21.06)
84.61 (10.72)	22.67 (4.55)	119.22 (9.23)	0	0
0	0	0	0	0

APPENDIX

(*Continued*)

Bird	Condition	B_{L1}	B_{R1}	B_{L2}	B_{R2}
	4	18.69 (8.39)	84.63 (11.99)	100.73 (5.11)	5.02 (6.76)
		6.21 (3.78)	27.29 (10.16)	81.29 (9.80)	2.43 (2.00)
		14.58 (4.69)	71.75 (7.60)	95.23 (3.46)	0.80 (1.07)
		2.08 (1.71)	14.82 (4.70)	69.52 (6.21)	1.81 (1.23)
	5	80.96 (7.98)	24.58 (4.84)	29.44 (6.06)	85.02 (7.93)
		50.79 (12.94)	21.76 (3.51)	15.07 (5.72)	41.35 (9.91)
		94.55 (7.01)	19.08 (4.75)	10.14 (3.88)	109.93 (5.95)
		47.60 (7.42)	14.61 (1.46)	8.80 (3.54)	35.67 (9.74)
A8	1	90.87 (4.64)	6.06 (1.06)	16.97 (3.54)	92.12 (6.37)
		80.71 (9.48)	9.34 (6.16)	14.73 (4.03)	86.35 (7.48)
		94.76 (7.34)	10.20 (2.99)	23.16 (5.29)	103.02 (8.95)
		46.98 (1.23)	17.79 (2.11)	10.59 (2.77)	51.82 (6.99)
		107.99 (5.51)	15.01 (3.56)	18.88 (5.56)	116.37 (4.55)
		39.51 (7.36)	15.61 (6.40)	8.71 (0.70)	41.41 (8.61)
		109.97 (4.36)	14.20 (4.47)	23.47 (6.74)	119.19 (7.60)
		74.08 (13.37)	10.83 (3.27)	22.16 (7.51)	68.73 (20.85)
		114.29 (5.32)	9.77 (1.43)	24.25 (5.77)	100.52 (5.91)
		54.30 (51.68)	8.05 (6.36)	10.67 (9.75)	46.53 (34.53)
	2	99.57 (7.87)	5.32 (1.15)	0.82 (0.67)	97.17 (10.13)
		87.84 (18.68)	10.15 (4.58)	1.05 (0.64)	74.25 (9.61)
		111.67 (4.35)	3.79 (2.00)	0.21 (0.15)	119.11 (7.03)
		56.48 (20.77)	4.71 (1.52)	0.07 (0.11)	80.68 (14.72)
		107.81 (3.69)	5.63 (1.58)	0.15 (0.24)	99.30 (5.21)
		48.56 (–)	3.88 (–)	0.44 (–)	86.86 (–)
		110.00 (6.16)	2.94 (0.66)	0.15 (0.32)	102.48 (2.51)
		44.66 (2.25)	2.62 (0.10)	0.18 (0.05)	62.21 (0.66)
		115.30 (4.04)	5.68 (2.26)	0.20 (0.42)	115.84 (3.57)
		36.13 (45.23)	2.05 (2.73)	1.13 (2.21)	33.87 (46.20)
	3	112.54 (3.29)	22.34 (4.97)	124.65 (5.67)	0.24 (0.47)
		56.72 (10.60)	2.35 (0.82)	54.59 (0.17)	3.99 (3.48)
		106.61 (5.78)	13.83 (4.87)	113.80 (8.46)	2.35 (1.53)
		54.28 (9.31)	2.50 (0.43)	54.69 (9.57)	2.69 (1.95)
		111.11 (7.24)	15.47 (1.85)	106.61 (11.86)	0.12 (0.22)
		59.31 (13.82)	1.60 (0.65)	55.36 (16.25)	0.41 (0.33)
		112.53 (5.03)	7.57 (1.62)	109.95 (3.10)	0.27 (0.57)
		80.65 (9.72)	11.89 (5.42)	97.01 (8.73)	0.34 (0.41)
		107.34 (3.73)	9.31 (3.88)	113.54 (5.28)	0.06 (0.18)
		66.83 (7.94)	13.01 (6.30)	90.77 (17.25)	0.58 (1.37)
		124.20 (3.21)	14.06 (5.12)	138.55 (3.54)	0.26 (0.54)
		58.07 (48.37)	13.58 (11.65)	60.22 (49.26)	0.80 (0.91)
	4	10.92 (5.65)	94.61 (12.04)	129.33 (15.76)	0.84 (1.61)
		6.10 (6.25)	43.52 (12.98)	111.27 (20.48)	1.52 (2.05)
		2.98 (3.23)	104.21 (19.72)	139.82 (31.13)	1.36 (2.53)
		1.92 (1.28)	37.07 (3.83)	86.49 (15.74)	0.30 (0.15)
	5	105.71 (10.37)	14.51 (2.24)	4.70 (2.56)	99.41 (7.45)
		58.30 (28.20)	31.30 (17.80)	11.63 (8.38)	38.00 (8.75)
		117.01 (10.92)	10.12 (4.01)	1.91 (1.60)	103.31 (5.46)
		81.24 (12.78)	12.78 (4.76)	2.50 (2.10)	37.94 (6.76)

APPENDIX

(Continued, Extended)

R_{L1}	R_{R1}	R_{L2}	R_{R2}	R_{BO}
0	28.74 (10.03)	117.26 (6.46)	0	0
0	22.85 (6.25)	115.32 (4.56)	0	269.25 (41.67)
0	24.09 (4.99)	114.88 (8.46)	0	0
0	18.05 (10.05)	115.28 (7.70)	0	529.71 (51.4)
78.91 (7.42)	28.36 (7.05)	0	39.26 (4.62)	0
76.82 (5.33)	32.31 (5.12)	0	38.83 (3.83)	270.61 (47.88)
85.02 (6.26)	29.37 (5.20)	0	39.67 (2.20)	0
76.23 (8.14)	29.13 (10.98)	0	36.42 (4.96)	551.58 (49.84)
83.11 (7.10)	14.75 (5.99)	17.76 (6.32)	80.51 (6.77)	0
80.80 (6.90)	21.77 (7.55)	17.78 (4.41)	81.94 (9.36)	136.30 (32.63)
86.36 (9.10)	21.37 (5.27)	23.55 (7.61)	82.29 (5.65)	0
65.12 (6.64)	36.90 (3.35)	10.70 (2.92)	75.08 (15.91)	490.14 (33.52)
85.87 (6.90)	21.37 (6.39)	17.34 (5.88)	80.52 (8.56)	0
64.71 (13.01)	28.03 (3.40)	17.22 (6.17)	73.12 (0.37)	632.06 (72.55)
85.75 (9.41)	25.85 (8.50)	23.95 (8.45)	79.08 (6.27)	0
78.12 (10.64)	22.58 (7.16)	21.81 (6.94)	84.55 (9.88)	300.63 (41.49)
81.17 (4.89)	20.87 (7.44)	23.55 (5.30)	82.78 (7.45)	0
0	0	0	0	0
81.20 (11.54)	20.40 (7.42)	0	115.39 (10.80)	0
83.53 (8.11)	20.91 (7.49)	0	110.56 (7.45)	113.67 (35.31)
87.76 (8.61)	21.83 (6.50)	0	114.86 (7.07)	0
83.32 (7.64)	17.84 (8.00)	0	117.78 (9.31)	282.48 (25.36)
83.15 (10.73)	21.75 (4.13)	0	119.23 (10.06)	0
73.38 (–)	21.58 (–)	0	113.87 (0.01)	564.71 (–)
81.92 (7.11)	17.79 (5.68)	0	117.27 (7.55)	0
93.99 (3.33)	17.49 (0.05)	0	106.72 (3.35)	560.65 (30.44)
80.35 (7.27)	22.19 (8.71)	0	116.82 (9.69)	0
0	0	0	0	0
81.95 (9.30)	17.79 (3.93)	117.75 (6.73)	0	0
79.01 (3.42)	2.14 (3.03)	106.72 (3.35)	0	507.17 (131.27)
84.98 (7.67)	21.81 (6.56)	114.38 (6.60)	0	0
79.21 (10.07)	4.32 (6.10)	109.09 (0.00)	0	544.06 (131.06)
87.01 (8.01)	17.45 (8.32)	116.33 (9.45)	0	0
90.44 (4.63)	1.44 (2.49)	112.32 (9.99)	0	519.71 (115.96)
83.77 (7.50)	11.25 (6.87)	120.17 (7.91)	0	0
79.92 (7.25)	15.57 (6.56)	121.62 (6.95)	0	145.33 (28.56)
87.78 (6.99)	15.25 (7.61)	121.64 (8.60)	0	0
82.55 (8.00)	13.43 (7.56)	115.35 (7.92)	0	277.93 (33.47)
85.41 (5.05)	15.18 (5.89)	121.14 (7.97)	0	0
0	0	0	0	0
0	30.80 (6.03)	120.19 (8.87)	0	0
0	28.27 (5.75)	112.96 (8.34)	0	283.95 (55.45)
0	27.87 (7.34)	118.24 (8.02)	0	0
0	28.08 (4.47)	113.90 (6.78)	0	551.61 (57.09)
83.09 (6.88)	28.43 (5.23)	0	40.54 (4.41)	0
64.33 (14.82)	37.32 (4.94)	0	38.83 (4.87)	292.06 (37.33)
86.53 (7.34)	30.76 (6.35)	0	38.83 (3.60)	0
79.78 (9.66)	24.68 (6.09)	0	36.42 (4.16)	539.51 (28.53)